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An Empirical Reevaluation of Absolute Pitch: Behavioral and Electrophysiological Measurements

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Abstract

■ Here, we reevaluated the "two-component" model of absolute pitch (AP) by combining behavioral and electrophysiological measurements. This specific model postulates that AP is driven by a perceptual encoding ability (i.e., pitch memory) plus an associative memory component (i.e., pitch labeling). To test these predictions, during EEG measurements AP and non-AP (NAP) musicians were passively exposed to piano tones (first component of the model) and additionally instructed to judge whether combinations of tones and labels were conceptually associated or not (second component of the model). Auditory-evoked N1/P2 potentials did not reveal differences between the two groups, thus indicating that AP is not necessarily driven by a differential pitch encoding ability at the processing level of the auditory cortex. Otherwise, AP musicians performed the conceptual association task with an order of magnitude better accuracy and shorter RTs than NAP musicians did, this result clearly pointing to distinctive conceptual associations in AP possessors. Most notably, this behavioral superiority was reflected by an increased N400 effect and accompanied by a subsequent late positive component, the latter not being distinguishable in NAP musicians. ■

INTRODUCTION

Absolute pitch (AP) is defined as the ability to either identify the pitch class (the chroma) of a tone or to produce a specific pitch without referring to a reference tone (Levitin & Rogers, 2005; Zatorre, 2003; Takeuchi & Hulse, 1993). This specific ability is different from the much more common relative pitch (RP) ability, which practically all musicians learn allowing them to identify or produce tone intervals. Although the research on AP has increased substantially in the last 120 years, the psychological, neurophysiological, and neuroanatomical underpinnings of this interesting ability are still far from being entirely understood.

Currently, there is unanimous agreement that AP is relatively discretely distributed in the population and that its prevalence strongly differs between cultures (Deutsch, Dooley, Henthorn, & Head, 2009; Deutsch, Henthorn, Marvin, & Xu, 2006; Keenan, Thangaraj, Halpern, & Schlaug, 2001; Gregersen, Kowalsky, Kohn, & Marvin, 1999; Miyazaki, 1988). More precisely, the prevalence of AP in the general population is estimated to be of about 0.01% (Baharloo, Johnston, Service, Gitschier, & Freimer, 1998). However, Asian people speaking tonal languages are more often considered to have AP (Gregersen et al., 1999). Moreover, professional musicians were previously shown to have a higher incidence of AP than nonmusicians (Deutsch et al., 2006, 2009; Keenan et al., 2001). This observation has led to a suggested relationship between musical training and AP ability, which is possibly driven by the timing of active exposure to music during childhood (Meyer et al., 2011; Zatorre, 2003; Schlaug, Jancke, Huang, & Steinmetz, 1995). In fact, although the debate on whether (and to which extent) AP abilities are genetically determined or rather develop under the influence of environmental factors like training (or even by an interaction between the two variables) is certainly not yet concluded (Levitin & Rogers, 2005; Vitouch, 2003; Zatorre, 2003), there is anyhow evidence indicating that the age of commencement of musical training may have an important influence on the development of AP (Meyer et al., 2011; Miyazaki & Ogawa, 2006; Russo, Windell, & Cuddy, 2003; Baharloo et al., 1998; Schlaug et al., 1995). This perspective is made a little more complicated by previous observations showing that not only musicians but even nonmusicians seem to have the faculty to process (at least partially) pitch absolutely, probably by accessing long-term memory representations. This is the case, for example, when musically untrained participants have to determine whether telephone dial tones (Smith & Schmuckler, 2008) and familiar television soundtracks (Schellenberg & Trehub, 2003) are played in the original key or participants are asked to sing familiar songs from memory (Levitin, 1994; Halpern, 1989).

Although it seems that everyone has at least some degree of AP (Levitin & Rogers, 2005; Zatorre, 2003), there are undoubtedly several important behavioral differences

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between AP possessors and nonpossessors. In this context, a main aspect differentiating between these two groups of individuals is that only AP possessors seem to have the explicit ability to associate musical tones with corresponding verbal and nonverbal labels (or other abstract codes; Levitin & Rogers, 2005; Zatorre, 2003). This discrepant ability between AP and non-AP (NAP) musicians becomes particularly evident, for example, when participants have to verbalize the pitch of a heard tone or to associate it with a note on a staff. Currently, there is some evidence showing that the left arcuate fasciculus, which is a fiber bundle stretching from the posterior supratemporal plane to frontal brain regions, may facilitate conceptual associations between auditory information and the corresponding labels (Loui, Li, Hohmann, & Schlaug, 2011; Oechslin, Imfeld, Loenneker, Meyer, & Jancke, 2010). Furthermore, it is still unclear whether small-world properties (i.e., local connectedness and global efficiency of information transfer) of left peri-sylvian brain regions may account for the more distinctive conceptual associations of AP musicians (Jäncke, Langer, & Hänggi, 2012; Loui, Zamm, & Schlaug, 2012) and whether cortical hyperconnectivity of superior temporal regions is specific to AP rather than to savant skills in general (Loui et al., 2011).

In terms of the proposed psychological processes, some believe that AP ability is related to an early "categorical perception" for pitch at the initial stage of auditory processing. During this process tones are thought to be automatically associated with nominal verbal labels (Siegel, 1974). An alternative to this "early categorization theory" has been proposed by Levitin and Rogers (2005), who postulated a two-component model of AP. According to this model, two different processes are operative during pitch processing in AP and RP musicians, namely "pitch memory" and "pitch labeling." Because pitch memory is widespread in the entire population (even in nonmusicians), they argue that it is not a typical feature of AP musicians. Pitch labeling on the other hand should be the specific ability that is present in AP musicians only. In the context of this model, the authors argue that there is no difference between AP possessors and NAP possessors in the early phase of tone perception.

Neurophysiological evidence for the two-component model comes from one brain imaging study and several EEG studies. In the brain imaging study of Zatorre, Perry, Beckett, Westbury, and Evans (1998), AP and RP musicians were asked to name tones or intervals while the CBF was measured. Interestingly, AP musicians demonstrated stronger CBF increases in the posterior dorsolateral pFC, whereas RP possessors activated this region only during interval naming. The dorsolateral pFC is known to be involved in conditional associative learning. Thus, the authors argued that AP processing should be characterized as the ability "to retrieve an arbitrary association between a stimulus attribute (the pitch of a sound) and a verbal label." In addition, the same authors proposed that this association would occur spontaneously and, therefore, form the basis for AP labeling. Participants without AP "would be unable to label isolated tones and, therefore, show no activity in this region." Interestingly, there was no difference between AP and RP musicians in terms of CBF in the primary or secondary auditory cortex. This specific result is also in line with a previous EEG study of Tervaniemi, Alho, Paavilainen, Sams, and Näätänen (1993), who did not reveal differences in the MMN between AP and NAP musicians during passive listening. By contrast, Ohnishi et al. (2001) using fMRI and demonstrated stronger hemodynamic responses in the planum temporale of AP possessors, compared with NAP musicians, to tones and melodies. There was even a strong correlation between the strength of hemodynamic responses in the planum temporale and the acuity of AP. Similar results were provided by an fMRI experiment (Schulze, Gaab, & Schlaug, 2009) that demonstrated stronger hemodynamic responses in the left STS, which is part of the secondary auditory cortex, in the early phase of memorization of pitches for AP musicians. Interestingly, in later phases, this difference was absent.

To date, there are also several electrophysiological studies that demonstrated an absent or smaller P300 component in AP musicians during pitch memory tasks (Crummer, Walton, Wayman, Hantz, & Frisina, 1994; Wayman, Frisina, Walton, Hantz, & Crummer, 1992; Klein, Coles, & Donchin, 1984; for a different finding, see Hirose et al., 2002). Because the P300 is an evoked response thought to reflect working memory processes, the smaller or absent P300 in AP musicians was interpreted as an indicator of reduced working memory involvement during pitch memory tasks in this group. Although the abovementioned studies emphasize neurophysiological differences between AP and NAP possessors for later processing stages, there are also some neurophysiological studies reporting differences even during early processing stages. For example, Itoh, Suwazono, Arao, Miyazaki, and Nakada (2005) computed evoked potentials in response to tones and provided evidence for a left posterior temporal negativity, which was only present in AP possessors at about 150 msec after tone presentation during tone-listening and pitch-naming tasks. Furthermore, on the basis of MEG registrations, Hirata, Kuriki, and Pantev (1999) found differences for the M100 dipole between AP and NAP musicians during tone perception. Finally, Wu, Kirk, Hamm, and Lim (2008) uncovered greater activation in AP possessors than in non-AP possessors in left and right auditory regions during pitch labeling.

Here, we empirically reevaluated the "two-component" model of AP by performing behavioral and EEG measurements in a sample of AP and NAP musicians. During EEG registration, the participants either passively listened to musical tones or performed a cross-modal conceptual association task requiring the subjects to evaluate whether musical tones and visually presented labels were congruent or noncongruent. In the case of a specific early perceptual

encoding ability (i.e., pitch memory) only present in AP musicians, we hypothesized that the early components of the auditory-evoked potentials (AEPs; e.g., the N1/P2 complex) would be different in AP musicians compared with NAP musicians. If on the other hand the later occurring associative memory component (i.e., pitch labeling) would be the pivotal process in AP musicians, we anticipated differences in later processing stages. In particular, based on previous work showing that the N400 (Kutas & Federmeier, 2011) and late positive component (LPC; Kutas & Federmeier, 2011; Friedman & Johnson, 2000) reliably represent the strength of cross-modal memory associations, we expected to find that AP musicians will manifest stronger N400 effects as well as increased LPC manifestations. The N400 component has previously repeatedly been shown to constitute an objective marker for investigating the conceptual relatedness between visual and auditory representations, such as, for example, graphemes and phonemes (Proverbio, Vecchi, & Zani, 2004) as well as written nouns and sounds (Goerlich et al., 2012). Furthermore, even so the exact functional processes reflected by the LPC are much less clear than those of the N400 (Friedman & Johnson, 2000), this component has been proposed to be driven by the allocation of memory resources (Chung, Tong, & McBride-Chang, 2012; Ohara, Lenz, & Zhou, 2006). Hence, the N400 and LPC are considered to be fruitful electrophysiological markers for investigating the associative memory component (i.e., pitch labeling) of AP. Most importantly, drawing on the premise that the skill to associate pitches with labels (and vice versa) is principally an attribute of AP possessors (second component), we expected that AP musicians will exhibit shorter RTs as well as increased sensitivity scores (d' values) in the conceptual association task.

METHODS

Participants

Fifteen professional AP (10 women and 5 men, mean age = 22.4 years, *SD* = 4.5 years) and 15 NAP (11 women and 4 men, mean age = 24 years, *SD* = 4 years) musicians were recruited from local music academies. All AP (5 violinists, 2 violists, 1 cellist, 3 pianists, 1 guitarist, 1 oboist, 1 flutist, and 1 vocalist) and NAP (3 violinists, 3 violists, 3 cellists, 1 pianist, 2 flutists, and 3 vocalists) musicians commenced their musical training before the age of 7 years; reported no past or current neurological, psychiatric, or neuropsychological problems; and denied consumption of illegal drugs or regular medication. According to the Annett Handedness Inventory (Annett, 1970), one participant per group was consistently left-handed, whereas the rest of the participants were consistent right-handers. The musicians were paid for participation, the local ethics committee approved the study, and written informed consent was obtained from all participants.

History of Musical Training

History of musical training was assessed by an in-house questionnaire previously used by our group (Elmer, Meyer, & Jancke, 2012a). This questionnaire was adopted to evaluate the age of commencement of musical practice, the primary instruments played by the musicians, the number of years of musical training, and the self-estimated number of training hours per week during every 3-year period of life (0–3, 4–6, 7–10, etc.). On the basis of the subjective data reported by the participants, we extrapolated the total number of training hours across lifespan for each participant.

Musical Aptitudes

All participants performed an auditory test (Advanced Measure of Music Audition) for examining their musical aptitudes as well as their musical achievement (Gordon, 1989). This procedure has previously been used by our group (Elmer et al., 2012a; Kühnis, Elmer, Meyer, & Jäncke, 2012; Ott, Langer, Oechslin, Meyer, & Jäncke, 2012) and consisted of 30 successive trials in which participants had to compare pairs of piano melodies and to decide whether the heard melodies were equivalent, rhythmically different, or tonally different.

AP Ability

To verify AP ability, the participants performed an adapted in-house test (Oechslin et al., 2010). During the test, participants listened to 108 piano tones presented in a pseudorandomized order and were instructed to write the tonal label on paper immediately after they heard the accordant tone (i.e., while hearing a 4 sec of Brownian noise). The presented tones ranged from C3 (tuning: A4 = 440 Hz) to B5. Accuracy was evaluated by counting the total number of correct responses. Semitone errors were counted as incorrect responses to increase discriminatory power. Each tone had a duration of 1 sec, and the ISI of 4 sec was filled with brown noise to increase task difficulty. The whole test unit was created by using Adobe Audition 1.5. (tv.adobe.com/de/product/audition/), performed by using a HP Laptop, and presented via in-ear Sennheiser headphones (HIFI, CX-350). Auditory stimuli presentation was controlled by the Presentation software (Neurobehavioral Systems, Version 14.5).

Cognitive Capability

To rule out differences in general cognitive capability between the two groups, we applied the KAI test (Kurztest für allgemeine Intelligenz; Lehrl & Fischer, 1992), which measures working memory and speed of information processing. During this test, the participants were instructed to read aloud meaningless sequences of 20 letters as quickly as possible as well as to repeat auditorily presented letters and digits increasing in length (up to

nine items). The KAI correlates about $r = .6$ with global IQ in healthy adults (Lehrl & Fischer, 1992).

Stimulus Material

Auditory Stimuli

The auditory stimuli presented during the EEG experiment were created with the FL Studio 9 software (Image Line Software BVBA, Sint-Martens-Latem, Belgium) and consisted of 14 different piano tones (Steinway Concert Grand Piano timbre) taken from the Garritan Personal Orchestra (MakeMusic, Inc., Eden Prairie, MN). The different piano tones covered the seven chromas from C to F# in Octaves 4 and 5 (tuning: A4 = 440 Hz), were converted to mono files (32-bit/44.1 kHz sample rate), logarithmically smoothed with a fall time of 20 msec to avoid an abrupt decay, normalized in amplitude, and had a duration of 500 msec. All acoustic manipulations were performed by using Adobe Audition 1.5 (Adobe Systems, Inc., San Jose, CA). During EEG measurements, the stimuli were presented to the participants at about 70 dB (Digital Sound Level Meter 329, Voltcraft) by using in-ear Sennheiser headphones (HIFI, CX-350). The presentation of the auditory stimuli and the recording of behavioral responses were controlled by the Presentation software (Neurobehavioral Systems, Albany, CA; version 14.5).

Visual Stimuli

The visual stimuli consisted of verbal (e.g., the written label "cis") and nonverbal labels (single quarter notes on a staff, written in treble clef) that were presented on the middle of a computer screen for a duration of 500 msec. We used both verbal as well as nonverbal labels to investigate putative influences of stimulus material on AP ability. The verbal labels consisted of German tone names corresponding to the seven chromas of the piano tones previously described. Because the verbal labels "dis" (D#) and "es" ($E^{\flat}$) describe the same piano tone and are equally common in musical notation, both labels were presented to the participants. This procedure resulted in eight different verbal labels, namely, "c," "cis," "d," "dis," "es," "e," "f," and "fis." The nonverbal labels consisted of 16 musical notes on a staff, were written in treble clef, and corresponded to the seven chromas of the piano tones. The musical notes $D^{\#}$ and $E^{\flat}$, which describe the same chroma, were both presented. Each note was depicted once in Octaves 4 and 5. The treble clef notation was chosen because it is the most commonly used notation, and all musicians reported to be familiar with it. Note pictures were created with Magic-Score Maestro 6.0 (DG Software, Lugansk, Ukraine). Musical notes as well as verbal labels were displayed centrally in black color on a white background. The presentation of the visual stimuli and the recording of the behavioral responses were controlled by the Presentation software (Neurobehavioral Systems; version 14.5).

Experimental Procedure

Before starting the experimental session, all participants performed the KAI test (Lehrl & Fischer, 1992) and completed the questionnaires on handedness, biographical data, and history of musical training. Afterward, the participants entered the main EEG session, which started with the passive listening condition and was followed by four conceptual association conditions consisting of the following associations: tone–verbal label, verbal label–tone, tone–note, and note–tone. The passive listening condition was intentionally presented previous to the conceptual association task for avoiding that the participants explicitly attempted to associate the heard tones with any symbols or labels. At the end of EEG measurements, each volunteer performed the test for musical aptitudes as well as the AP test. The entire experimental session lasted approximately for 3 hr.

Passive Listening Condition

The same auditory stimuli used in the conceptual association task were delivered to the participants in a randomized order (each of the 14 piano tones was presented six times, resulting in totally 84 piano tones) with an ISI of 1000 msec. During the passive listening condition, the participants were instructed to focus a fixation cross presented in the middle of the screen, to pay attention to the auditory stimuli, and to not explicitly associate the heard tones with any verbal or nonverbal labels. In a post-experimental debriefing, all participants confirmed that they followed the instructions.

Conceptual Association Task

Subsequent to the passive listening condition, participants entered the conceptual association task consisting of four different runs presented in a pseudorandom order. At the beginning, each participant performed 10 practice trials to familiarize with the task. In each of the four runs, an auditory prime stimulus was followed by a visual target stimulus, or vice versa, resulting in the following four experimental conditions: tone as prime and verbal label as target (TL), verbal label as prime and tone as target (LT), tone as prime and note as target (TN), and note as prime and tone as target (NT). Each condition consisted of 88 congruent and 88 incongruent trials presented in a random order. Half of the participants of each group started with the verbal label conditions (TL and LT) followed by the nonverbal conditions (TN and NT), whereas the other half proceeded vice versa. Furthermore, to increase discriminatory power between the two groups, the incongruent trials consisted of labels, notes, and tones that differed at most by two semitones.

During the task, participants were instructed to indicate as quickly and accurately as possible by pressing two response buttons with the right fore and middle fingers

whether the stimulus pairs were congruent or incongruent. Immediately after the response occurred, the next trial was presented. If the participants did not respond within a time range of 2000 msec, the trial was automatically terminated and the next one commenced. The duration of each conceptual association condition (i.e., run) varied approximately between 8 and 11 min, depending on the subject's response speed. Auditory and visual presentation and collection of behavioral responses were controlled by the Presentation software (Neurobehavioral Systems, Version 14.5). Figure 1 illustrates an example of the time course of the tone–label and note–tone conditions.

EEG Recording and Analysis

Preprocessing

The high-density EEG (128 channels) was recorded with a sampling rate of 250 Hz and a band pass filter of 0.1–100 Hz (Electrical Geodesics, Eugene, OR). Electrode Cz served as on-line reference, and impedances were kept below 30 kΩ. After recording, the electrodes in the outermost circumference were removed and noisy channels interpolated, resulting in a standard 111-channel electrode array (Perrin, Pernier, Bertrand, Giard, & Echallier, 1987). Afterward, the data were off-line-filtered with a low-pass filter of 30 Hz, eye movements were corrected by using an independent component analysis (Jung et al., 2000), and remaining artifacts were removed manually by using the Brain Vision Analyzer software package (Brain Vision Analyzer 1.05; www.brainproducts.com/downloads.php). All electrodes were rereferenced to a virtual average reference, and the data were segmented into 1200 msec epochs. A baseline correction was applied to the −200 to 0 msec prestimulus period. For each subject, target stimulus, and condition (i.e., TL, TN, LT, and NT) epochs were averaged and grand-averages were computed. Furthermore, to avoid multiple comparisons between neighboring electrodes and to increase signal-to-noise ratio, data were pooled into seven ROIs at frontal (left frontal, middle frontal, and right frontal), central (left central, central, and right central), and parietal scalp sites (Eichele, Nordby, Rimol, & Hugdahl, 2005). Figure 2 indicates the spatial configuration of the ROIs.

AEPs Elicited during the Passive Listening Condition

To compare perceptual encoding of musical tones in the auditory cortex of AP and NAP musicians, auditory-evoked N1/P2 peak amplitudes and latencies were evaluated. These AEPs have previously been consistently shown to constitute an objective measure for assessing auditory cortex functions in musicians (Baumann, Meyer, & Jancke, 2008; Meyer, Baumann, & Jancke, 2006; Shahin, Bosnyak, Trainor, & Roberts, 2003) and nonmusicians (Mayhew, Dirckx, Niazy, Iannetti, & Wise, 2010) with remarkable fidelity. Furthermore, there is strong evidence showing that early ERPs (overlapping with the N1/P2 complex) are particularly sensitive to cross-modal association (Elmer, Meyer, & Jancke, 2012b; Jancke, Rogenmoser, Meyer, & Elmer, 2012). In fact, recent neuroimaging and electrophysiological studies (Besle, Bertrand, & Giard, 2009; Murray & Spierer, 2009; Teder-Salejarvi, McDonald, Di Russo, & Hillyard, 2002; Giard & Peronnet, 1999) militate in favor of the view that the synthesis of sensory and cognitive information can occur in brain regions that are usually thought of as being responsive to sensory-specific stimuli. In addition, a very recent EEG study (Schirmer, Soh, Penney, & Wyse, 2011) could show that the N1/P2 complex is sensitive to a preceding prime, this specific study (as well as several other studies) clearly showing that early brain responses reflect memory processes as well. This perspective is further

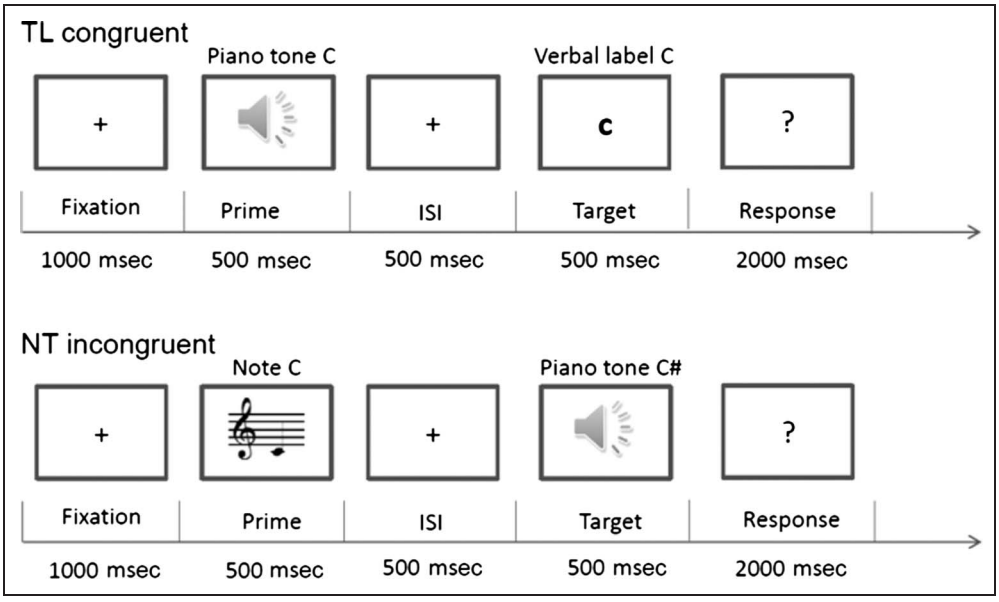

Figure 1. The timing of the conceptual association task is illustrated for the congruent tone–label (TL, top) and incongruent note–tone (NT, bottom) conditions.

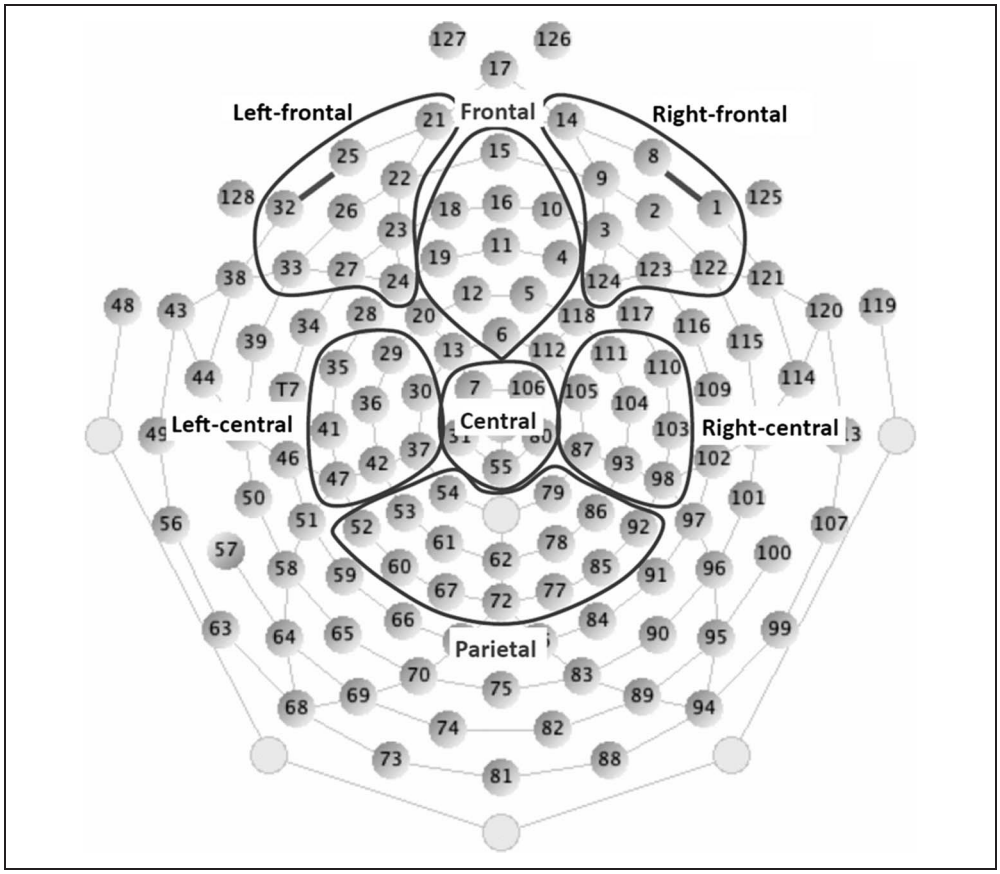

Figure 2. Spatial arrangement of the ROIs on the surface of the scalp.

supported by the fact that the N1/P2 complex overlaps in time with the MMN, a preattentive brain response originating from auditory-related brain regions and reflecting sensory memory processes (Näätänen, Astikainen, Ruusuvirta, & Huotilainen, 2010).

Maximal N1 and P2 amplitudes were automatically identified in the time range between 100–200 (N1) and 200–300 (P2) msec by using the Brain Vision Analyzer software package (Brain Vision Analyzer 1.05; www.brainproducts.com/downloads.php). The labeled peaks were additionally confirmed or rejected by visual inspection. Maximal N1 and P2 peak amplitudes and latencies were evaluated at the ROI position where voltage values were most pronounced, namely, at the central ROI. Figure 3 shows genuine N1/P2 responses at the central ROI position for the two groups.

Event-related Potentials Elicited during the Conceptual Association Task

Brain responses to congruent and incongruent targets were computed separately for each condition (i.e., TL, LT, TN, and NT). In addition, for each participant, condition, and ROI difference waves (DW; see Figure 4) were calculated by subtracting brain responses to congruent trials

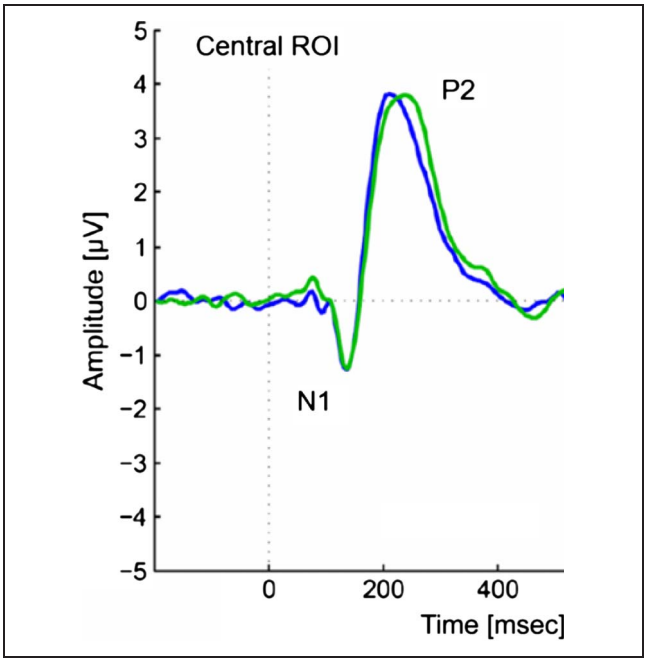

Figure 3. Auditory-evoked N1/P2 potentials in response to piano tones during the passive listening condition (central ROI position). *x* axis = time in milliseconds; *y* axis = mean amplitude (μV); blue line = AP musicians; green line = NAP musicians.

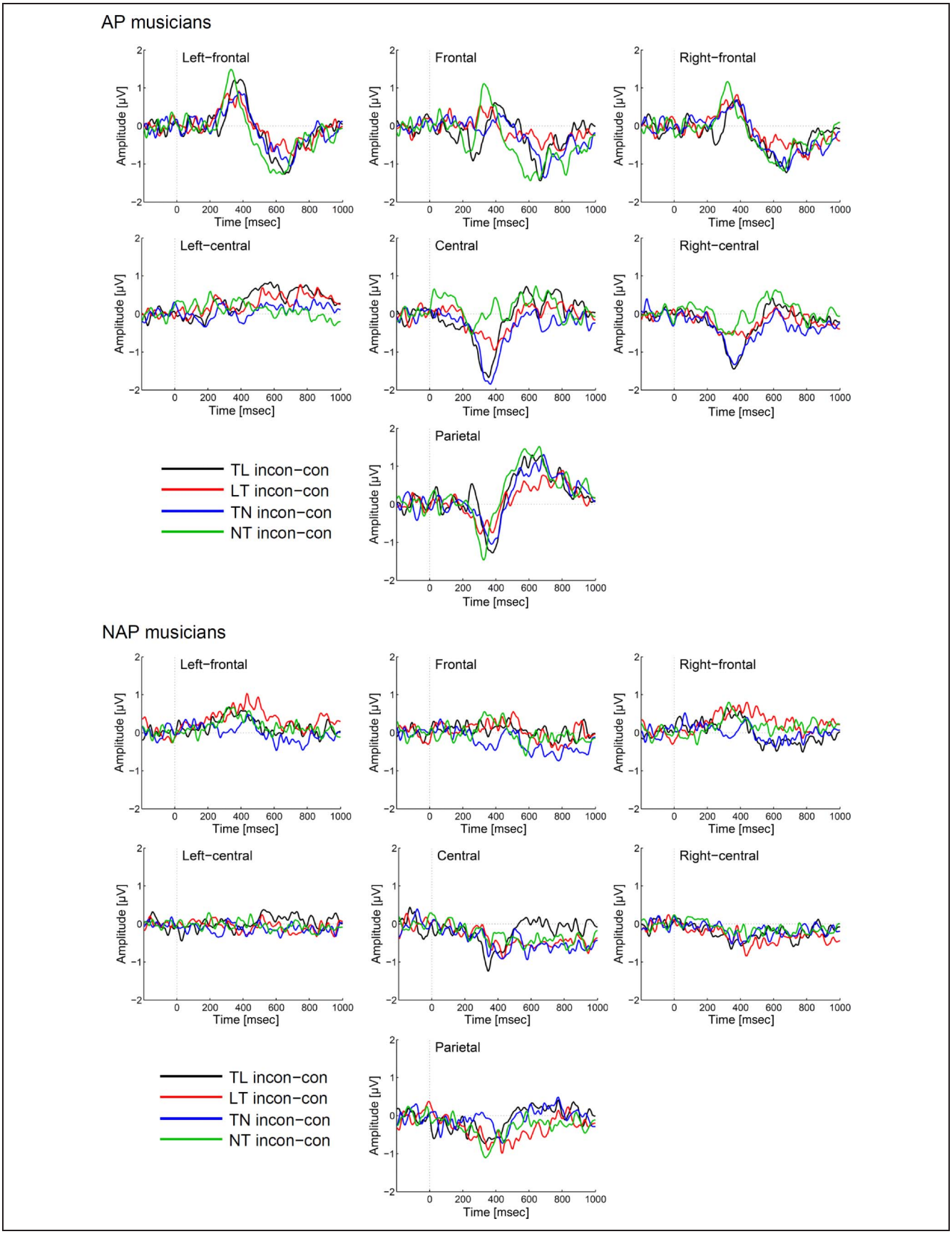

Figure 4. Difference waveforms in response to targets (incongruent minus congruent trials) elicited during the four experimental conditions in the two groups (top, AP musicians; bottom, NAP musicians) at each ROI position. Conditions: TL = tone–verbal label; LT = verbal label–tone; TN = tone–note; NT = note–tone. ROI positions: left frontal, frontal, right frontal, left central, central, right central, parietal.

from those to incongruent trials. On the basis of previous work showing that the N400 and LPC components are robust markers of associative memory functions across a variety of stimulus material (Kutas & Federmeier, 2011; Friedman & Johnson, 2000), we evaluated mean N400 and LPC amplitudes in response to congruent and incongruent targets in the following time windows: 250–450 msec (N400) and 450–600 msec (LPC; see Figure 4). Taking advantage of the information provided by the topographic voltage distribution maps (DWs; see Figure 5), group differences in the 250–450 latency band were analyzed at the central, right-central, and parietal ROI positions. Otherwise, based on the observation of spatially heterogeneous scalp distributions maps in both groups in latency bands from 450 to 600 (see Figure 5), mean LPC amplitudes were evaluated at all seven ROI positions.

Statistical Analyses

Statistical analyses were performed by using the SPSS 19 software package (SPSS, Inc., IBM, Armonk, New York). Behavioral sensitivity scores (d'; Stanislaw & Todorov, 1999) and RTs were evaluated by computing three-way ($2 \times 2 \times 4$) ANOVAs (repeated-measures), with the between-subject factor of Group (AP, NAP) and the two within-subject factors of Congruency (congruent, incongruent) and Condition (TL, LT, TN, NT). Similar three-way ANOVAs (Group × Congruency × Condition) were executed for evaluating mean ERP amplitudes in response to the target stimuli, separately for each latency band (N400 and LPC) and ROI position. The Greenhouse–Geisser correction for nonsphericity was applied where appropriate. Significant interaction effects were further inspected by using post hoc t tests. Maximal N1/P2 peak amplitudes and latencies elicited during the passive listening condition were evaluated at the central ROI position by means of t tests for independent samples (two tailed). Correlation analyses (Spearman's rho) were used for investigating potential relationships between behavioral and autobiographical data.

BEHAVIORAL RESULTS

AP Test

The professional musicians who participated in this study were recruited by means of the self-reported ability to perceive pitches absolutely (AP) or even not (NAP). To confirm this ability, all participants performed an adapted in-house AP test (Oechslin et al., 2010) performed with piano tones. In line with the self-reported AP ability of the participants, this specific test confirmed that AP musicians performed significantly better than NAP musicians ($U = 0, z = -4.69, p < .001$). In fact, AP musicians reached a mean score of 96.7% correct responses (SD = 4.5, range = 86.1–100), whereas NAP participants performed with an average score of 18.2% correct responses (SD = 13.2, range = 2.8–42.6). Importantly, the performance of the NAP musicians significantly differed from chance level (chance level = 8.33% correct responses; $t(14) = 2.90, p < .05$). This specific result indicates that NAP musicians still exhibit some elemental abilities to explicitly associate pitches with labels. Figure 6 indicates clearly distinct AP score distributions between the two groups.

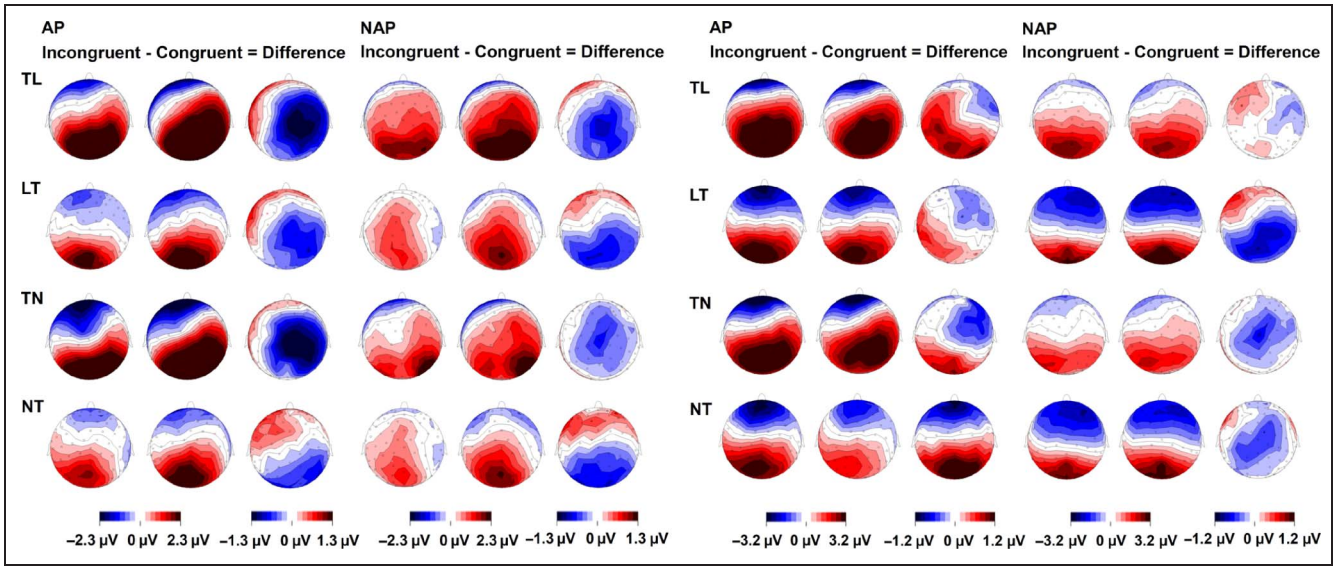

Figure 5. Topographic voltage distribution maps associated with the N400 (left) and LPC (right) components in response to targets for each experimental condition (first row, tone–label; second row, label–tone; third row, tone–note; fourth row, note–tone) are depicted separately for incongruent and congruent trials and the two groups (AP and NAP). The third column of each figure shows the topographic voltage distribution of the DWs (incongruent minus congruent trials). Please note that the voltage values are differently scaled for N400 and LPC. The same is the case for congruent/incongruent trials and DWs.

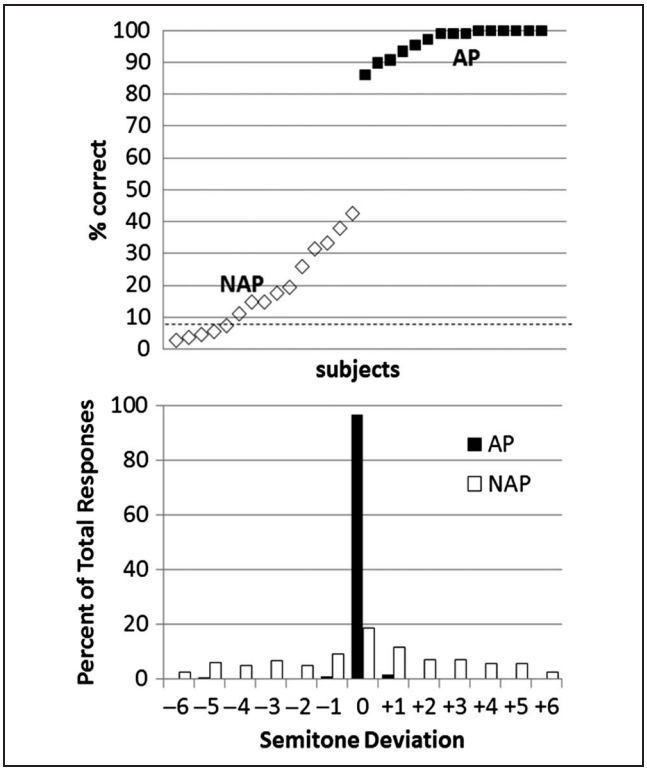

Figure 6. Percentage of correct responses of each participant in the AP test (top) as a function of semitone deviation (bottom). Black = AP musicians; white = NAP musicians. The dashed line indicates chance level.

Biographical Data, Cognitive Capability, and Musical Aptitudes

The statistical evaluation of age (AP mean age = 22.4 years, *SD* = 4.5; NAP mean age = 24.0 years, *SD* = 4.0), musical aptitudes (AP mean score = 68.7, *SD* = 4.8; NAP mean score = 68.0, *SD* = 4.3), general cognitive capability (AP mean score = 128.9, *SD* = 7.7; NAP mean score = 126.2, *SD* = 8.3), age of training onset (AP mean age = 5.2, *SD* = 1.3; NAP mean age = 5.5, *SD* = 1.5), total number of years of training (AP mean number of years = 17.2, *SD* = 4.3; NAP mean number of years = 18.5, *SD* = 4.3), total number of training hours across lifespan (AP mean number of hours = 14030, *SD* = 7323; NAP mean number of hours = 13674, *SD* = 7173), and mean training hours per year (AP mean number of hours = 822, *SD* = 420; NAP mean number of hours = 713, *SD* = 258) did not reveal significant group differences.

Conceptual Association Task

RTs (only correct trials) were evaluated by means of a three-way (2 × 2 × 4) ANOVA (repeated-measures), with the between-subject factor of Group (AP, NAP) and the two within-subject factors of Congruency (congruent, incongruent) and Condition (TL, LT, TN, NT). This statistical procedure yielded a significant main effect of Congruency, $F(1, 28) = 17.38$, $p < .001$, which originated from shorter RTs in response to congruent (mean [*M*] = 901 msec, *SD* = 317) compared with incongruent targets (*M* = 969 msec, *SD* = 303). As expected, the same statistical analysis revealed a significant main effect of Group, $F(1, 28) = 25.40$, $p < .001$. AP musicians (*M* = 727 msec, *SD* = 223) responded faster than NAP musicians (*M* = 1143 msec, *SD* = 229). The main effect of Condition was also significant, $F(3, 84) = 12.08$, $p < .001$, indicating longer RTs in the LT condition compared with the other three conditions.

The statistical evaluation of accuracy data (d' scores) revealed that in both groups mean or median d's significantly differed from chance level in all four conditions (all $p < .01$, one-sample *t* tests or Wilcoxon signed rank tests in the case of nonnormality). Furthermore, a three-way (2 × 2 × 4) ANOVA (repeated-measures) performed on d' scores yielded a significant main effect of Group, $F(1, 28) = 99.14$, $p < .001$, with AP musicians (*M* = 5.27, *SD* = 1.38) showing considerably higher d' values than NAP musicians (*M* = 1.12, *SD* = 0.83).

ELECTROPHYSIOLOGICAL RESULTS

Passive Listening Condition

The piano tones presented during the passive listening condition elicited genuine N1 (~130 msec) and P2 (~220 msec) AEPs with a maximal voltage distribution over central scalp sites in both groups (see Figure 3). Group-wise comparisons of maximal N1 and P2 peak amplitudes and latencies were performed at the central ROI position by means of *t* tests for independent samples (two-tailed). We did not reveal group differences in N1 ($t(28) = -.491$, $p = .62$) and P2 ($t(28) = .038$, $p = .97$) amplitude nor in N1 ($t(28) = .431$, $p = .67$) and P2 ($t(28) = -1.2$, $p = .24$) latency. Hence, these results clearly indicate that perceptual pitch encoding in the auditory cortex of AP and NAP musicians did not differ.

To get additional information, we also performed map-by-map comparisons of the topographic ERP maps of scalp potentials across the two groups (Lehmann, 1987). Statistical significance for each pair of maps was assessed non-parametrically with a randomization test (Manly, 1997), which in addition corrects for multiple testing. The details of this procedure, called topographic ANOVA (TANOVA), are reported elsewhere (Strik, Fallgatter, Brandeis, & Pascual-Marqui, 1998). The topographic ANOVA was performed in the latency band between 0 and 400 msec by using the LORETA software (www.uzh.ch/keyinst/loreta.htm). In line with the above-described AEP analyses, this additional statistical procedure did not reveal significant group differences.

ERPs in Response to the Targets: N400

As visible in Figure 5, the N400 effect (DWs) was maximal over central-posterior scalp sites, AP musicians showing

increased magnitudes compared with NAP musicians. Furthermore, in the two conditions with auditory primes and visual targets (TL, TN), the scalp maps showed a central voltage distribution, which was more pronounced in the AP group and slightly lateralized to the right side. However, in the conditions with visual primes and auditory targets (LT, and especially NT), the N400 effect was associated with a posterior voltage distribution in the two groups, AP musicians showing a slightly increased right lateralization pattern. Mean voltage values in latency bands from 250 to 450 msec were subjected to three-way ANOVAs (2 × 2 × 4, repeated-measures), with the between-subject factor of Group (AP, NAP) and the two within-subject factors of Congruency (congruent, incongruent) and Condition (TL, LT, TN, NT). On the basis of the topographic voltage distribution (DWs, see Figure 5), separate ANOVAs were calculated for the central, right-central, and parietal ROIs. For clarity, significant main and interaction effects are reported separately.

Main Effects: N400

Statistical analyses yielded a significant main effect of Congruency at central, $F(1, 28) = 30.45$, $p < .001$, right central, $F(1, 28) = 56.00$, $p < .001$, and parietal ROI positions, $F(1, 28) = 37.46$, $p < .001$. This main effect of Congruency originated from more negative mean amplitudes in responses to incongruent compared with congruent targets. Furthermore, we revealed a significant main effect of Condition at right central, $F(1.74, 48.79) = 26.68$, $p < .001$, and parietal ROI positions, $F(1.66, 46.46) = 6.90$, $p < .01$. As visible in Figure 7 (i.e., first two columns of each group), this effect originated from a less positive voltage distribution at parietal and right central scalp sites during the LT and NT conditions in comparison with the other two conditions.

Interaction Effects: N400

The same statistical procedure described above yielded a significant Group × Congruency interaction effect at the right central ROI position, $F(1, 28) = 7.36$, $p < .05$. This interaction originated from an increased N400 effect (i.e., difference between incongruent and congruent trials) in the AP group. Because the topographic maps implemented in Figure 5 arouse the suspicion that this specific interaction was principally driven by the TL and TN conditions, additional two-way ANOVAs (Group × Congruency) were run separately for each condition at the right-central ROI position. As expected, significant Group × Congruency interaction effects only appeared in the two conditions where the tone acted as prime (TL: $F(1, 28) = 7.20$, $p < .05$; TN: $F(1, 28) = 9.25$, $p < .01$). Finally, the main three-way ANOVA also revealed a significant Condition × Congruency interaction effect at the central, $F(2.27, 63.66) = 6.35$, $p < .01$, and right central ROI positions, $F(3, 84) = 4.55$, $p < .01$. As visible in Figures 5 and 7, these interaction effects originated

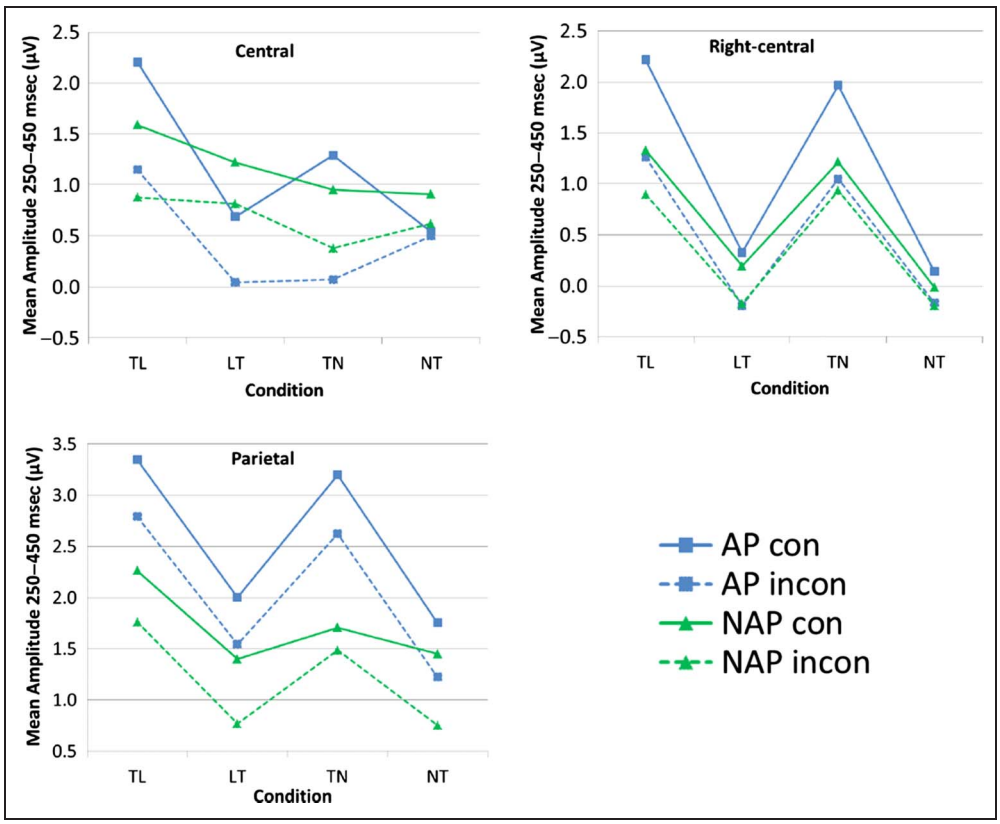

Figure 7. Mean N400 amplitudes in response to congruent (continuous lines) and incongruent (dashed lines) targets for each group (blue, AP; green, NAP) and ROI position (central, right-central, and parietal).

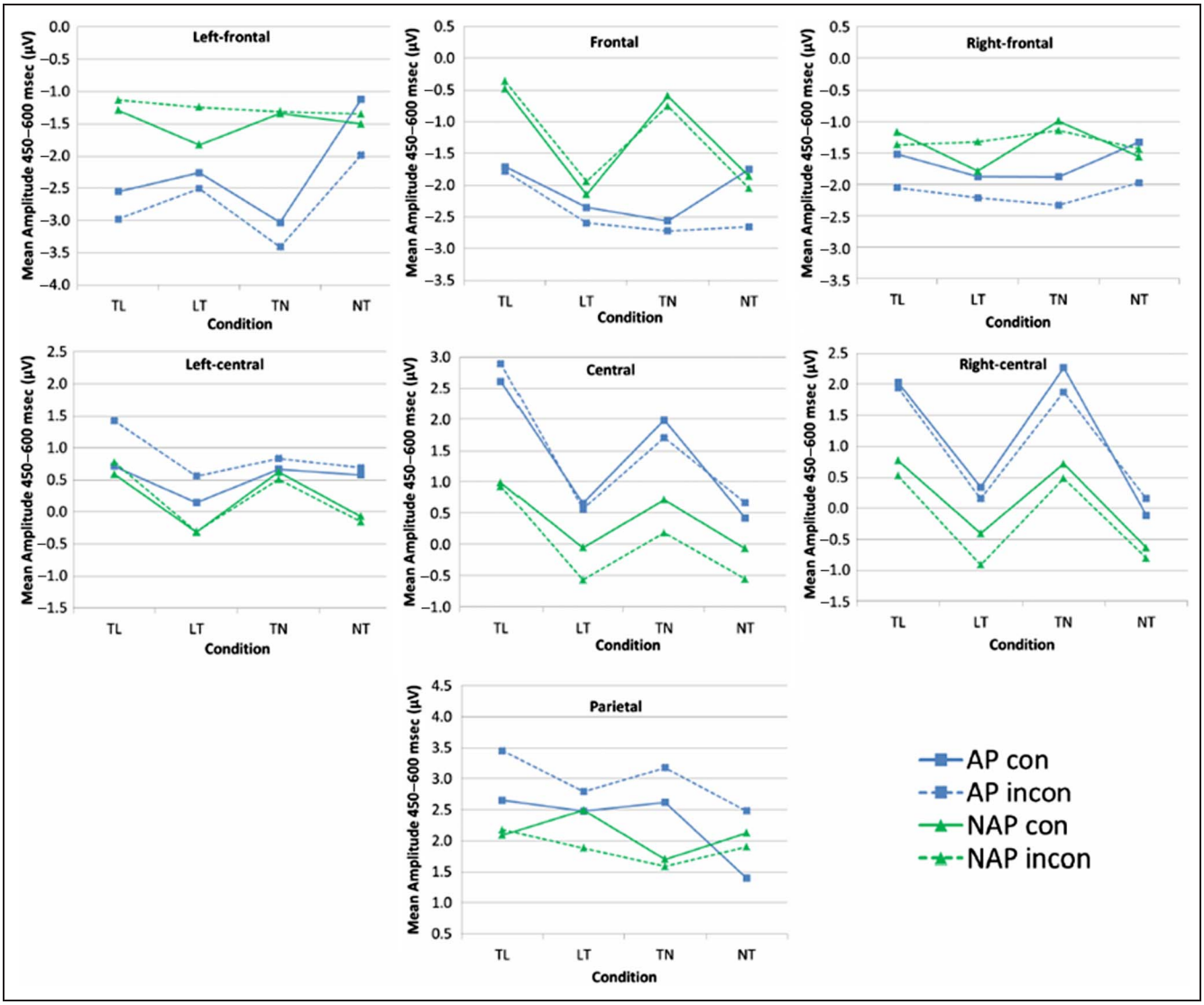

Figure 8. Mean LPC voltage amplitudes in response to congruent (continuous lines) and incongruent (dashed lines) targets for each group (blue, AP; green, NAP) and ROI position (left frontal, frontal, right frontal, left central, central, right central, and parietal).

from a reduced N400 effect at central scalp sites during the NT condition.

ERPs in Response to the Targets: LPC

The EEG difference waveforms depicted in Figure 4, as well as the topographic voltage distribution maps of Figure 5, clearly indicate a divergent pattern of brain responses between the two groups to the targets. In this context, the AP musicians showed a positive voltage distribution at central-posterior scalp sites, whereas a corresponding pattern was not distinguishable in the NAP group. In fact, NAP musicians showed an ongoing negativity over central-posterior scalp sites with a reversal of polarity at anterior electrodes rather than an LPC-like voltage distribution. This specific brain signature of NAP musicians was comparable to that elicited in the latency band from 250 to 450 msec and associated with the N400 effect (see Figure 5).

Main Effects: LPC

Mean voltage values in the latency band from 450 to 600 msec (LPC) were subjected to three-way ANOVAs ($2 \times 2 \times 4$, repeated-measures), with the between-subject factor of Group (AP, NAP) and the two within-subject factors of Congruency (congruent, incongruent) and Condition (TL, LT, TN, NT). Given that the two groups revealed clearly distinct and heterogeneous voltage distributions (see Figure 5), the LPC was evaluated for all seven a priori-defined ROI positions.

Statistical analyses yielded a main effect of Congruency at right central, $F(1, 28) = 5.81$, $p < .05$, left central, $F(1, 28) = 4.51$, $p < .05$, right frontal, $F(1, 28) = 5.49$,

$p < .05$, and parietal ROI sites, $F(1, 28) = 4.33$, $p < .05$. Most importantly, we revealed a main effect of Group at the central, $F(1, 28) = 5.85$, $p < .05$, and right central ROI positions, $F(1, 28) = 11.54$, $p < .01$. This main effect of Group originated from significantly more positive mean amplitudes in AP possessors compared with NAP musicians. Finally, we also uncovered a main effect of Condition at central, $F(1.90, 53.14) = 14.74$, $p < .001$, right central, $F(1.81, 50.68) = 41.16$, $p < .001$, and left central ROI sites, $F(2.00, 55.94) = 8.38$, $p < .01$. The main effects of Condition resulted from more negative mean amplitudes in response to auditory targets (LT and NT conditions) as compared with visual ones (TL and TN conditions; see Figure 8).

Interaction Effects: LPC

The same three-way ANOVAs yielded a Group × Congruency interaction effect at left central, $F(1, 28) = 4.52$, $p < .05$, right frontal, $F(1, 28) = 8.84$, $p < .01$, left frontal, $F(1, 28) = 10.10$, $p < .01$, and parietal, $F(1, 28) = 15.75$, $p < .001$, ROI positions. As visible from Figures 5 and 8, this interaction effect originated from clearly distinct brain responses to congruent and incongruent trials between the two groups. In fact, AP musicians showed a central-posterior positivity (LPC) with an inversion of polarity at frontal scalp sites, whereas the brain responses of NAP musicians were rather associated with an N400 effect that was similar to that elicited in latency bands from 250 to 450 msec. Finally, we revealed significant Condition × Congruency interaction effects at the right-central, $F(3, 84) = 3.35$, $p < .05$, left central, $F(3, 84) = 3.82$, $p < .05$, and parietal ROI positions, $F(3, 84) = 3.88$, $p < .05$.

RELATIONSHIP BETWEEN BIOGRAPHICAL AND BEHAVIORAL DATA

Putative relationships between AP test, conceptual association task (d' scores and RT), and number of training hours

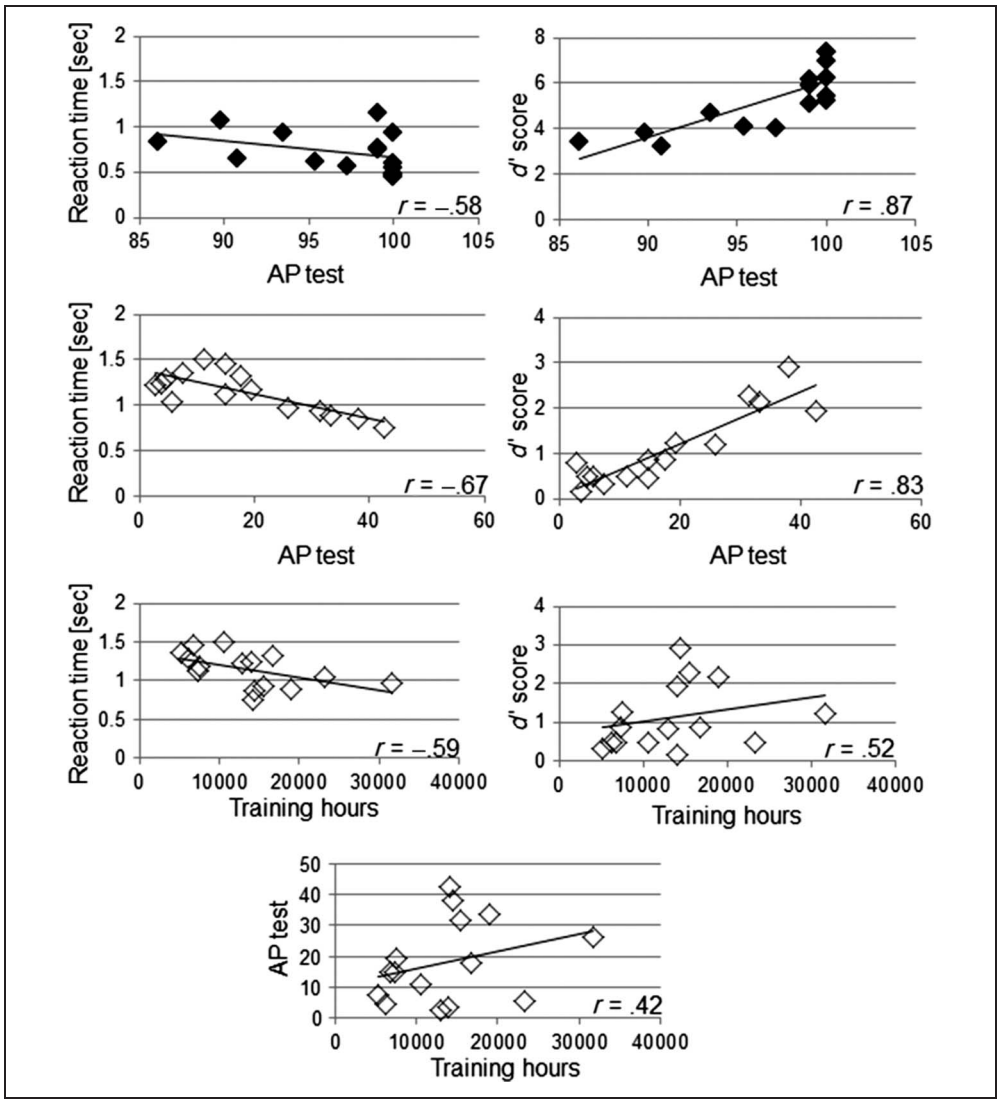

Figure 9. Significant correlations. AP musicians are depicted in black; NAP musicians are in white.

across lifespan were examined by performing within-group correlative analyses (Spearman's rho, one tailed). RT and d' scores were averaged over congruent and incongruent trials as well as over the four experimental conditions to reduce the number of statistical tests and the corresponding experiment-wise type I error rate. Certainly, this proceeding could suffer of a certain lack of precision, but otherwise it enables to illustrate important biographical/behavioral relationships, which will remain undetected by correcting for multiple comparisons.

Correlative analyses showed significant relationships between AP test performance and RT/d' scores within both groups (AP musicians: $r_{\text{AP test\_RT}} = -.585$, $p < .05$; $r_{\text{AP test\_}d'} = .872$, $p < .001$; NAP musicians: $r_{\text{AP test\_RT}} = -.674$, $p < .01$; $r_{\text{AP test\_}d'} = .836 < .001$). The correlations between the number of training hours across lifespan and behavioral data (AP/RT/d') reached significance (NAP musicians: $r_{\text{training\_RT}} = -.596$, $p < .01$; $r_{\text{training\_}d'} = .529$, $p < .05$) or at least evidenced a statistical trend (NAP musicians: $r_{\text{training\_AP test}} = .420$, $p = .06$) within the NAP group only. In summary, these results primarily indicate that in the two groups the behavioral performance during the AP test was predictive for the ability to perform the conceptual association task. In addition, the relationship we revealed within the NAP group between the number of training hours across lifespan and behavioral data (AP/RT/d') indicates that NAP musicians can increase their associative memory ability with training. All correlations are depicted in Figure 9.

DISCUSSION

Until now, several attempts have been made to improve the understanding of the perceptual and/or cognitive mechanisms enabling professional musicians to explicitly associate tones with verbal or nonverbal labels. On the basis of the excellent time resolution of EEG as well as of the functional meaning of event-related brain responses, we postulated that early categorical perception for pitches at the initial stage of auditory processing (first component of the model) should be manifested in time windows overlapping with the N1/P2 complex. In addition, we presumed that the associative memory component of AP, namely, "pitch labeling," is reflected by the N400 and LPC components. In fact, both brain responses have previously been shown to be sensitive to cross-modal associations and memory processes in general (Chung et al., 2012; Kutas & Federmeier, 2011; Ohara et al., 2006; Friedman & Johnson, 2000; Kutas & Hillyard, 1984). Our results support the basic principles postulated by the "two-component" model but at the same time provide some important extensions and specifications. To the best of our knowledge, this work constitutes the first empirical study devoted to systematically reevaluate the "two-component" model of AP by applying both behavioral and electrophysiological measurements.

Behavioral and Biographical Data

The behavioral and biographical data clearly point to a comparable history of musical training, musical aptitude, and cognitive capability between the two groups of musicians. Hence, it is not plausible to assume that one of these variables may have influenced the data in a particular direction. Otherwise, in line with our hypothesis, the AP test not only resulted in a distribution with two clearly distinct clusters representing the two groups (Figure 6, top), but also successfully predicted participants' performance during the conceptual association task. In fact, AP musicians performed significantly better than NAP musicians (as reflected by higher d' scores and shorter RT across all experimental conditions). Furthermore, within-group correlation analyses performed between AP values and RT/d' scores clearly indicated that those musicians with increased AP ability also performed better on the conceptual association task. Consequently, one may argue that the AP test and the conceptual association task rely, at least in part, on common associative memory mechanisms. Furthermore, it is important to mention that NAP musicians not only performed above chance level on both the AP test and the conceptual association task but also showed shorter RTs in response to congruent as opposed to incongruent trials. These results are in accordance with a previous behavioral study (Hsieh & Saberi, 2008) and clearly indicate that some elemental forms of cross-modal memory associations are still present in NAP musicians. Most notably, the elemental AP ability of NAP musicians seems to improve with training, as provided by the significant correlations we revealed between the self-estimated number of training hours across lifespan and behavioral data. Taken together, our data confirm the notion that the associative memory component constitutes a specific attribute of AP possessors. However, the ability to perceive pitch absolutely cannot be understood as a dichotomy but rather implies a continuum along which the strength and direction of memory associations vary as a function of training, at least in NAP musicians.

EEG Data

N400

The N400 is a negative-going waveform that peaks at approximately 400 msec after stimulus onset at central-posterior scalp sites and is typically examined by comparing brain responses to different conditions (or items) that match or mismatch in terms of conceptual category membership (Kutas & Federmeier, 2011). So far, an impressive amount of work took advantage of the N400 component for investigating conceptual category membership and memory associations across a wide range of topics, including language processing (Elmer, Meyer, & Jancke, 2010; Federmeier, McLennan, De Ochoa, & Kutas, 2002; Kutas & Hillyard, 1984), object, face, action, and gesture processing (Wu & Coulson, 2011; van Elk, van Schie, &

Bekkering, 2010; Bentin & Deouell, 2000), mathematical cognition (Luo, Liu, He, Tao, & Luo, 2009), music processing (Painter & Koelsch, 2011; Steinbeis & Koelsch, 2011), as well as different kinds of cross-modal conceptual associations (Wu, Athanassiou, Dorjee, Roberts, & Thierry, 2012). Meanwhile, it is generally acknowledged that the N400 amplitude becomes smaller when the incoming information is expected or congruent with the previous conceptual framework, irrespective of the experimental paradigm used. By contrast, when the conceptual information is incongruent with the previous context, or even unexpected, then the N400 amplitude increases dramatically (Kutas & Federmeier, 2011; Federmeier et al., 2002).

In the present work, we made use of the N400 component for investigating the organizational principles underlying cross-modal conceptual associations in AP and NAP musicians. As a main result, we found a significant Group × Congruency interaction effect at the right central ROI position. This result clearly indicates an increased N400 effect in AP musicians, in comparison with NAP musicians, irrespective of the experimental condition. In fact, from Figure 7, it becomes visible that the increased N400 effect in AP musicians can be described as a more pronounced difference (Δ) between brain responses to incongruent and congruent trials. Therefore, from a pragmatic point of view, enlarged Δ values support the conclusion of a much more distinctive neural coding of conceptual associations in AP possessors. Interestingly, Figures 5 and 7, as well as the additional post hoc analyses we performed, indicate that the increased Congruency effect we observed in AP musicians was particularly pronounced during the TL and TN conditions. In fact, the tone acted as prime in exactly these two conditions. This result further implicates that the associations between musical tones and labels are much more distinctively coded than those in the opposite direction, and probably driven by experience. In fact, AP musicians appear to more often engage their AP ability to associate tones with labels than in the opposite case.

Another important result of our work concerns the main effect of Congruency we revealed at central, right-central, and parietal ROI positions. This main effect originated from more negative mean N400 magnitudes in responses to incongruent as compared with congruent targets, irrespective of group affiliation. Notably, this result is in line with the behavioral data and indicates that not only AP musicians but also NAP possessors demonstrate some elemental forms of cross-modal memory associations. The notion that the human brain is able to associate musical sounds with other conceptual representations is of course not novel and has been described by other authors who investigated musicians (Steinbeis & Koelsch, 2008) as well as nonmusicians (Gordon, Schon, Magne, Astesano, & Besson, 2010; Daltrozzo & Schon, 2009; Orgs, Lange, Dombrowski, & Heil, 2006; Koelsch et al., 2004). For example, Orgs and colleagues (2006) measured a sample of nonmusicians while tones played by a variety of instruments were paired with either congruent or incongruent visually presented verbal labels (e.g., a piano tone and the word "piano") and provided evidence for reliable bidirectional N400 effects. In addition, N400 effects were previously also shown to occur when musical excerpts (Daltrozzo & Schon, 2009; Koelsch et al., 2004) or single chords (Steinbeis & Koelsch, 2008, 2011) are paired with semantically related or unrelated words (e.g., dissonant chord and word "hate") or even when sung words are repeated with the same versus a different melody (Gordon et al., 2010).

Taken together, our electrophysiological N400 results are in line with the assumption postulated by the "two-component" model. In fact, AP possessors showed a more distinctive neural coding of conceptual associations than NAP musicians. However, we provide important specifications. The fact that also NAP musicians showed a significant Congruency effect clearly supports the notion that the ability to build conceptual associations between notes and tones can be likewise present in musicians without AP, although to a much lesser degree. This perspective is hardened by the behavioral results (i.e., d') and points to a flowing transition between the strength of conceptual associations in AP and NAP musicians.

LPC

The LPC is as a positive-going waveform, which is typically elicited between 400 and 800 msec poststimulus onset with a maximal current distribution over central-posterior scalp sites (Friedman & Johnson, 2000). Because LPC manifestations appear at relatively late stages of cortical processing, this specific ERP component has previously been associated with cognitive rather than sensory processes. In fact, the LPC has been proposed to reflect a variety of top–down processes like expectancy (Regnault, Bigand, & Besson, 2001), explicit recognition memory (Friedman & Johnson, 2000), recollection (Olichney et al., 2000; Smith & Guster, 1993), successful retrieval, structural reanalysis and repair functions across a wide range of stimulus material, as well as semantic and episodic memory functions (Friedman & Johnson, 2000). Although the specific cognitive processes reflected by this ERP, as well as its independence from the P300 component, are still a matter of debate (Kutas & Federmeier, 2011; Friedman & Johnson, 2000), to date there is at least agreement that the LPC is linked to strategic and effortful aspects of cognitive processing (Friedman & Johnson, 2000; Swaab, Brown, & Hagoort, 1998; Vanpetten, Kutas, Kluender, Mitchiner, & Mcisaac, 1991). In this context, the LPC is assumed to reflect the general ability of the human brain to amplify weak-meaning relationships (Kandhadai & Federmeier, 2010).

From Figures 4 and 5, it becomes visible that only AP musicians showed distinct LPC manifestations over central-posterior scalp sites, with an inversion of polarity at anterior electrodes. In fact, this specific pattern of brain

responses was not at all distinguishable in NAP musicians who rather showed an N400-like topographic voltage distribution similar to that elicited in latency bands from 250 to 450 msec. The statistical analyses confirmed this observation by revealing a main effect of Group at central and right central ROI positions, as well as a Group × Congruency interaction effect at right-frontal, left-frontal, left-central, and parietal ROI sites (see Figure 8). Certainly, we can only speculate about the intrinsic meaning of LPC manifestations in AP possessors. Notably, the fact that a similar voltage distribution pattern (i.e., posterior positivity) was not discernible in NAP musicians leads us to suggest that the LPC constitutes a salient electrophysiological marker distinguishing between AP and NAP musicians. Therefore, we propose that the sustained N400-like processing mode of NAP musicians may account for their elemental and more implicit (i.e., latent) ability to access cross-modal conceptual associations, whereas the LPC rather reflects the neuronal signature of explicit and more stable memory associations in AP possessors. In this context, we may speculate whether LPC manifestations may be involved in amplifying weak-meaning relationships during conceptual association tasks (Kandhadai & Federmeier, 2010).

Our results are compatible with a previous paper (Besson, Faita, & Requin, 1994) showing that LPC measures were larger in musicians than nonmusicians, but only when an explicit decision about the congruency of terminal notes was required from the participants. Although in this study we measured musicians with and without AP instead of musicians and nonmusicians, the common denominator of the two studies is the observation that LPC amplitudes seem to increase as a function of musical expertise. Certainly, we cannot exclude the possibility that the differential LPC responses we revealed between the two groups were more likely driven by expectation rather than by task-driven conceptual associations. Otherwise, it should be considered that such expectation processes can only be engaged when conceptual associations between labels and tones are already established within the brain. In other words, without established conceptual associations between tones and labels, it is certainly impossible to generate faithful expectations. A further point that should be mentioned is that between-group LPC differences could also result from task difficulty, a variable previously shown to influence the morphology of this ERP component (Besson et al., 1994; Johnson, 1986; Hillyard, Squires, Bauer, & Lindsay, 1971). However, as previously argued by Besson and colleagues (1994), this would be more likely the expression of expertise rather than that of task difficulty. Finally, we want to emphasize that the paradigm we used in this study fundamentally diverges from those of previous EEG studies on AP. In fact, Wu et al. (2008) presented sine wave tones to AP and NAP musicians and only focused on early stages of auditory processing in latency bands overlapping with the N1 component. In addition, although Itoh and coworkers analyzed both early and late event-related responses in AP and NAP musicians during passive listening and naming tasks (Itoh et al., 2005), the authors focused on the association between sine wave tones and verbal labels only (i.e., the participants vocally reported the pitches of the stimuli as either do, re, or mi after hearing a cue). This study is novel for several reasons. First of all, we used piano tones instead of sinus tones as stimuli, this specific experimental approach enabling a higher ecological validity of the results. In addition, we tested bidirectional conceptual associations between tones and labels by using both verbal and nonverbal stimuli. A further novelty of our study is that we were able to show that the sustained N400-like processing mode of NAP musicians may account for their elemental and more implicit (i.e., latent) ability to access cross-modal conceptual associations, whereas the LPC rather reflects the neuronal signature of explicit and more stable memory associations that are unique of AP possessors.

Structure–Function Relationship in AP Possessors

In the present work, we only focused on the temporal dynamics reflecting AP "perception" and pitch "labeling." However, to date there is growing evidence indicating that these two processes are mediated by distinctive brain regions and associated with specific anatomical white (Loui et al., 2011; Oechslin et al., 2010) and gray (Wengenroth et al., 2013; Jäncke et al., 2012) matter architectures. In fact, in a very recent study, Wengenroth et al. (2013) used functional and structural MRI, as well as magnetoencephalography and could show that gray matter volume of the right Heschl's gyrus was highly correlated with AP proficiency. In addition, right-hemispheric auditory-evoked fields (i.e., N1 and P2 responses) were increased in the AP group, and fMRI analyses provided evidence for distinct AP-specific networks mediating AP "perception" (right planum temporale) and pitch "labeling" (secondary somatosensory and premotor areas, as well as left-hemispheric frontal operculum) mechanisms. Interestingly, by using structural MRI, Jäncke and colleagues showed that AP is associated with a significantly increased local gray matter connectivity in peri-sylvian areas (planum temporale, planum polare, Heschl's gyrus, lateral aspect of the superior temporal gyrus, STS, pars triangularis, and pars opercularis), which are known to be involved in higher-order auditory processing (including working memory or semantic memory processes). Similar results were also reported by Loui et al. (2011), who used diffusion tensor imaging and tractography. The authors measured hyperconnectivity in bilateral superior temporal lobe structures of AP possessors. Notably, the volume of tracts connecting left superior temporal gyrus to left middle temporal gyrus predicted AP performance. In a further diffusion tensor imaging study, Oechslin et al. (2010) reported that AP is characterized by a greater left than right asymmetry of fractional anisotropy in core fibers of the superior longitudinal fasciculus, a fiber tract linking posterior temporal and frontal brain regions. Within the

left hemisphere, superior longitudinal fasciculus volume was positively correlated with error rate in an AP test (but only within the group of AP possessors). Taken together, these previous anatomical studies provide evidence for gray and white matter anatomical changes in auditory-related and frontal brain regions supporting higher-order auditory processing, memory, and conceptual associations in general.

Conclusion

In the present work, we used a combined electrophysiological and behavioral approach for reevaluating the "two-component" model of AP. We show for the first time that the sustained N400-like processing mode of NAP musicians accounts for their elemental and latent ability to access cross-modal conceptual associations, whereas the LPC clearly reflects the neuronal signature of explicit and more stable associative memory representations in AP possessors.

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